Behav Ecol Sociobiol (1988) 23:401–406

Behavioral Ecology and Sociobiology

Relatedness among nestmates in a primitively social wasp, *Cerceris antipodes* (Hymenoptera: Sphecidae)

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Received April 18, 1988 /Accepted August 31, 1988

Summary. Kin selection, acting through high levels of relatedness, may be an important promoter in the evolution of nest sharing. *Cerceris antipodes* is a sphecid wasp that shares nests in contrast to the majority of sphecids where only one female occupies a nest. Nest sharing results from females remaining in their natal nests and females moving to already occupied nests. Average relatedness among nestmates of *C. antipodes* was calculated from allele frequencies of phosphoglucomutase to determine whether nests were usually shared by close relatives. Relatedness among nestmates was high (0.5 to 0.6) at one aggregation in two consecutive years. Preferential association of relatives away from the natal nest can be inferred from these high values combined with the frequency of nest switching observed. Estimates of relatedness were lower (about 0.3) and associated with large standard errors at 3 other aggregations. Inbreeding and relatedness between neighbouring nests were only significant at the aggregation with the fewest females. This may be a result of the small effective population size. The levels of relatedness observed are consistent with kin selection through relatedness being an important factor in the evolution of nest sharing.

Introduction

Relatedness is a central concept in sociobiological theory (Hamilton 1964; Wilson 1971, 1975; Markl 1980; Michod 1982; Bennett 1987). The degree of relatedness between individuals is one determinant of how they will interact. Kin selection, especially through its dependence on relatedness, has been invoked to explain the evolution of many types of social behaviour (Wilson 1975; Davis 1984; Brown 1983; Trivers 1985; Smuts et al. 1986). Kin selection, acting through the high levels of relatedness between sisters in haplodiploid species, has been touted as the reason for the frequent evolution of eusociality in the Hymenoptera (Wilson 1971; Starr 1979; Trivers 1985; but see Andersson 1984). However, kin selection depends not only on relatedness but also on the ability of individuals to assist relatives to reproduce (Hamilton 1964; West Eberhard 1975).

Relatedness can only be a significant factor in promoting nest sharing, a first step in the evolution of eusociality, when levels of relatedness are greater than the cost to benefit ratio in the kin selection equation, that is $r > c/b$. Relatedness among individuals sharing nests has been calculated for more than 25 eusocial species. Estimates of relatedness have varied from nil in some ants (Pamilo 1982; Pamilo and Rosengren 1984) to more than 0.7 in some primitively eusocial bees and wasps and some ants (Crozier 1973; Metcalf and Whitt 1977; Crozier et al. 1987; Have et al. 1988). These estimates demonstrate that, even in eusocial species nestmates are not necessarily close relatives.

Of most relevance to the question of the evolution of social behaviour in the Hymenoptera is the degree of relatedness among nestmates in primitively social species. Schwarz (1986; 1987) has provided the only such estimates. For the primitively social bee, *Exoneura bicolor*, he calculated average relatedness among females in nests that were reused from one summer to the next and in nests that were cofounded by up to eight females. In both situations the average relatedness was close to 0.5, a value which suggests relatedness is involved in nest sharing.

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Cerceris antipodes Smith is a sphecid wasp that shares nests, does not have a reproductive division of labour, and its therefore primitively social (Alcock 1980; Evans and Hook 1986; McCorquodale 1988). In most species of sphecid wasps, and in by far the majority of *Cerceris* species, only one female occupies a nest. In *C. antipodes*, and several other species of *Cerceris*, nest sharing results from two processes (Alcock 1975; Kurczewski and Miller 1984; Elliott et al. 1986; Evans and Hook 1986; Hook 1987). Firstly, nests are occupied continuously for many months to a few years. This allows emerging adult females to share a nest with those females already present, presumably often close relatives (Alcock 1980; Evans and Hook 1986; Hook 1987; McCorquodale 1988). Second, some females switch from one nest to another occupied nest. This presumably results in nests being occupied by unrelated females. The combination of these two processes, remaining in the natal nest and switching nests, could lead to either closely related or unrelated females sharing nests.

Here I present estimates of average relatedness among nestmates in *C. antipodes.* Average relatedness between neighbouring nests and inbreeding were also calculated to see if population structure reduced effective relatedness of nestmates. Relatedness estimates were made using analyses that allow the use of electrophoretic data without major *a priori* assumptions about polygyny, polyandry or inbreeding (Pamilo and Crozier 1982; Crozier et al. 1984; Pamilo 1984; Bennett 1987). The major aim of this study is to determine if nestmates of *C. antipodes* are related and if this level of relatedness will significantly affect the cost/benefit ratio in the kin selection equation.

Materials and methods

Wasps

Adults of *Cerceris antipodes* were collected at nesting aggregations near Warrah Trig (Warrah) in Brisbane Water National Park (33° 33′ S, 151° 17′ E) and at Camp Pincham (Pincham) in Warrumbungle National Park (31° 18′ S, 149° 01′ E), New South Wales, Australia, from January 1985 until February 1987. All of the aggregations were located in December 1984 or January 1985. The three aggregations at Warrah (referred to as Warrah 1, 2 and 3) were within 1.5 km of each other along dirt tracks through heath woodland. Oincham is 500 km northwest of Warrah in the drier inland of New South Wales. The aggregation at Pincham was located along dirt tracks through dry sclerophyll woodland. These wasps and those at Warrah 1 were the subjects of behavioural observations during the three summers. Despite the difference in vegetation and climate, the behaviour and natural history of *C. antipodes* was similar at the two locations (McCorquodale 1988).

In 1985 males and females were collected at Warrah and Pincham for electrophoretic screening for polymorphic enzyme loci. Further collections in 1986 and 1987 were made over one to three days by placing clear cups over the nests for the duration of the wasps' active period. All females from nests with one to eight females were collected at Warrah 1 and 2 in 1987 and Pincham in 1987. Only females from nests with two or more females were collected at Warrah 1 in 1986 and Warrah 3 in 1987. Thus, for some nests females of two different generations were collected, while from other nests females of only one generation were collected. Wasps were kept cool until the evening, when they were killed in a freezer. The specimens were kept in a freezer for one to 10 days until transport to Canberra, where they were kept at −70° C until electrophoresed. All nests were mapped at each aggregation. From these maps the nearest neighbour of each nest was determined.

Electrophoresis

The wasps collected in 1985 were electrophoresed on cellulose-acetate plates. These samples were run several times and stained for 18 enzyme systems. The techniques of Easteal and Boussy (1987) were used as a guide for buffer and stain preparation. Only phosphoglucomutase (PGM) and adenylate kinase were variable and only PGM had allozymes at frequencies suitable for relatedness analysis. The head and thorax of wasps collected later than 1985 were ground in a grinding buffer (Water, EDTA, Mercaptoethanol and NADP), centrifuged, electrophoresed on cellulose-acetate plates in a CAEA buffer at pH 7.2 and stained for PGM (Easteal and Boussy 1987). A positive and negative control (PGM and Hexokinase, Malate dehydrogenase or Glucose-6-phosphate dehydrogenase) were run on most plates.

Three electromorphs (Fast-F, Medium-M and Slow-S) of PGM migrating anodally were distinguished. As expected in a haploid, all individual males had only one band and all three variants were found in the males. Females had either one or two bands. Single bands were interpreted as homozygotes and double bands as heterozygotes. Two to five of the 10 individuals from each plate were run a second time with individuals of at least two other plates. Individuals from up to five different samples were run on the same plate. These comparisons showed that the same variants were present in the five samples. The frequencies of the three electromorphs were compared among years at Warrah 1 and among aggregations in 1987 using a G Test with Williams correction (Sokal and Rohlf 1981).

Relatedness analyses

Average relatedness among wasps sharing the same nest was calculated using the genotypic correlation coefficient of Pamilo (1984, see equation 4). Two point estimates of relatedness and their standard errors were calculated using a jack-knife procedure. B1 weighted nests equally, while B2 weighted individuals equally. Similarly, F1 and F2 are point estimates of inbreeding, weighting nests and individuals equally. Average relatedness between nearest neighbour nests was also calculated (see equation 10 in Pamilo 1984). All calculations of relatedness and inbreeding estimators were performed using a computer programme written by R.H. Crozier (University of New South Wales) and modified for use of IBM compatible PC's by M.P. Schwarz (La Trobe University).

All point estimates of relatedness and inbreeding were tested against the null hypothesis that they were equal to 0. A one-tailed *t*-Test was used because only results above 0 were expected. Comparisons between estimates were made with t-Tests, either one or two-tailed depending on the situation. For these tests the degrees of freedom were based on the number of nests sampled from the aggregation (Crozier et al. 1984). This method assumes no selection on the locus used. Frequencies of presumed genotypes did not differ from those expected under Hardy-Weinberg equilibrium at any of the five aggregations (All Chi-square tests, 2df, $P > 0.1$). Ideally estimates of relatedness from electrophoretic data should be based on at least 10 colonies, with the most common allozyme at each locus at frequencies of less than 0.9, and be based on several loci or several aggregations (Pamilo and Crozier 1982; Pamilo 1984; Wilkinson and McCracken 1985; Bennett 1987). Here the PGM allozyme frequencies were within the acceptable range and more than 10 nests were used. Samples from four aggregations and two samples from one of those aggregations were employed, compensating for using only one locus.

Results

Variation among aggregations

Frequencies of the three allozymes varied among the aggregations (Table 1). Warrah 3 was the only aggregation that lacked the slow electromorph. Frequencies of the allozymes were similar among the three years at Warrah 1 (G-test, $G = 3.76$, 4 *df*, $P > 0.1$). However there were differences among the three aggregations at Warrah in 1987 ($G = 18.49$, 4 *df*, $P < 0.01$). In pairwise tests, each aggregation was different from the other two (1 and 2, $G = 9.52$, 2 *df*, $P < 0.01$; 1 and 3, $G = 11.79$, 2 *df*, $P < 0.01$; 2 and 3, $G = 6.31$, $P < 0.05$). These three aggregations were within 1.5 km of each other, with Warrah 1 about midway between the other two. The other aggregation, Pincham, was located more than 500 km north-west. Despite the distance, the allozyme frequencies at Pincham were indistinguishable from those at Warrah 2 and 3 ($G = 0.07$, $G = 5.83$, 2 *df*, $P > 0.05$). Allozyme frequencies at Pincham were different from those at Warrah 1 ($G = 9.63$, 2 *df*, $P < 0.01$). These comparisons were based on equal weighting of each female in the aggregation. It is appropriate to weight each female equally, since *C. antipodes* nests often contain several females capable of reproducing (McCorquodale 1988). Also, allozyme frequencies based on weighting each nest equally were similar and produced similar results.

Relatedness and inbreeding

The average relatedness among females sharing a nest was high at some aggregations and lower at other aggregations (Table 2). Most estimates of in-

Table 1. Frequencies of the three allozymes of phosphoglucomutase at four aggregations of *Cerceris antipodes*

Aggregation	Date	Fast	Medium	Slow	Females	Nests
Warrah 1	8 Jan to 15 Feb 85	0.36	0.62	0.02	21	12
Warrah 1	20 Feb to 4 Mar 86	0.31	0.65	0.04	95	27
Warrah 1	16–31 Jan 87	0.36	0.57	0.07	65	30
Warrah 2	3–7 Feb 87	0.23	0.75	0.02	59	24
Warrah 3	21 Jan 87	0.34	0.66	0.00	54	16
Pincham	3–4 Jan 87	0.23	0.75	0.02	50	28

Table 2. Estimates of average relatedness (B1, B2) and inbreeding (F1, F2) among females sharing a nest and average relatedness between nearest neighbour nests, at four nesting aggregations of *Cerceris antipodes*. B1 and F1 were calculated weighting each nest equally. B2 and F2 were calculated weighting each female equally. Standard errors are in parentheses below each estimate. The number of nests and females electrophoresed at each aggregation are in parentheses side each aggregation. All estimates have been tested against the null hypothesis that they are equal to zero, using a one-tailed t-test, $^{*}P < 0.05$, $^{**}P < 0.01$

Aggregation	Date	Within Nests				Nearest Neighbour	
		B1	B2	F1	F2	B1	B2
Warrah 1 (27/95)	1986	0.52**	0.51**	0.19	0.20*	−0.31	−0.31
		(0.11)	(0.11)	(0.11)	(0.10)	(0.10)	(0.12)
Warrah 1 (20/55)	1987	0.64**	0.62**	0.18	0.13	0.18	0.13
		(0.16)	(0.14)	(0.16)	(0.15)	(0.13)	(0.11)
Warrah 2 (20/55)	1987	0.28	0.29	0.19	0.20	0.04	0.04
		(0.29)	(0.30)	(0.19)	(0.19)	(0.04)	(0.04)
Warrah 3 (16/54)	1987	0.31*	0.25*	0.25*	0.23*	0.24**	0.23**
		(0.13)	(0.13)	(0.12)	(0.12)	(0.06)	(0.06)
Pincham (15/37)	1987	0.30	0.34	0.22	0.13	−0.02	−0.02
		(0.26)	(0.23)	(0.18)	(0.19)	(0.09)	(0.09)

breeding and relatedness between neighbouring nests were low and not significantly different from 0 (Table 2). Estimates based on both equal weighting of nests and equal weighting of individuals were similar (Table 2). In only one instance was the estimate based on one weighting statistically significant when the other was not (Warrah 1, 1986, F1 and F2, Table 2).

A high level of relatedness among nestmates, with estimates of more than 0.5, was evident in both the 1986 and 1987 samples at Warrah 1 (Table 2). Estimates of relatedness between neighbouring nests at Warrah 1 were not significantly greater than 0. One of the four inbreeding estimates was significantly greater than 0 (Table 2). These data indicate nest sharing by close relatives.

At Warrah 3 the estimates of average relatedness among females sharing nests, of inbreeding and of the relatedness between nearest neighbour nests were significantly greater than 0 (Table 2). At Warrah 2 and Pincham the average relatedness among females sharing nests was estimated to be about 0.30, although neither were significantly different from 0 (Table 2). The relatedness between neighbouring nests was estimated to be much lower, although not significantly different, partly because of the large standard errors associated with the estimates. Inbreeding estimates were also low and not significantly different from 0 at Warrah 2 and Pincham.

Discussion

Female *C. antipodes* that share a nest tend to be related. The average level of relatedness among nestmates varied among aggregations. The higher estimates of about 0.5 and 0.6 at Warrah 1, are consistent with a mother and her female offspring sharing a nest. Females of *C. antipodes* are long lived and reside in a nest for several weeks, longer than the time it takes for an egg to mature into an adult (McCorquodale 1988). The most likely scenario resulting in relatives sharing a nest is young females emerging and remaining in the nest with their mother and older siblings. About 15% of all females at Warrah 1 switch nests (McCorquodale 1988). This is a high frequency considering the high levels of relatedness. It is possible that females switch preferentially to nests occupied by relatives. I have observed more than one female from one nest move to the same non-neighbouring nest twice. This suggests that kin selection promotes preferential association with relatives away from the natal nest. Such preferential associations with kin have been demonstrated in other species of primitively social and primitively eusocial Hymenoptera (West Eberhard 1969; Strassman 1979; Schwarz 1986, 1987).

Estimates of average relatedness among nestmates, from Warrah 2 and Pincham, were lower than expected if mothers and their daughters share nests. These estimates had large standard errors and therefore were not significantly different from 0 or 0.75. Three processes reduce relatedness among nestmates: nest switching, more than one female laying eggs in a nest and multiple mating by females. At all aggregations 15–30% of females switched nests and most females in a nest were capable of laying eggs (McCorquodale 1988). Relatedness estimates of around 0.3 are approximately those expected if nests are shared by equal numbers of cousins and sisters and about half the nests include an unrelated joiner. However, the large standard errors preclude distinguishing between this scenario and either nests shared by nonrelatives or nests shared by mothers and their daughters.

The large standard errors in the relatedness estimates at two of the aggregations suggest that there was significant variation in average relatedness among nestmates among nests. Presumably at Warrah 2 and Pincham some nests were shared by unrelated females and other nests by closely related females. Nonrelatives sometimes do share nests as demonstrated by the extreme case of a nest shared by two species of *Cerceris* (McCorquodale and Thomson 1988). Whether the behaviour of *C. antipodes* varies with these variations in relatedness is of considerable interest. Eusocial ants, bees and wasps can recognize kin (Greenberg 1979; Post and Jeanne 1982; Carlin and Hölldobler 1983; Getz and Smith 1983) and in many situations exhibit preferential behaviour towards kin (e.g. Gamboa et al. 1985; Strassmann 1985). It is not clear if *C. antipodes* can recognize kin and act preferentially towards them. More direct methods of determining relatedness between pairs of individuals are needed to answer this question.

Variation in relatedness among aggregations is evident in estimates from a variety of other Hymenoptera and a subsocial beetle (Pamilo 1982; Pearson 1983; Pamilo and Rosengren 1984; Crozier et al. 1987; McCauley et al. 1987) and is likely in *C. antipodes*. Studies of *C. antipodes* behaviour at Warrah 1, at another site at Warrah (Alcock 1980), at Pincham and in Queensland (Evans and Hook 1986) reveal differences in nest switching, levels of aggression and oocyte development (McCorquodale 1988, in press). McCauley et al. (1987)

point out that variation in relatedness can result in quite different rates of social evolution in different geographic areas.

Most estimates of inbreeding were very low, with only two of the estimates significantly greater than 0. Only at Warrah 3 was inbreeding important. This was by far the smallest aggregation, increasing from about 12 nests in January 1985 to about 25 nests by January 1987. The small population size may be the cause of the high level of inbreeding and the lack of the slow allozyme. This aggregation also produced the only evidence of relatedness between neighbouring nests. Relatedness between nests is unlikely to reduce effective relatedness (Crozier et al. 1984) among nestmates in a species such as *C. antipodes*. There is little interaction between neighbouring nests and there is no territory centred on the nest. Foraging takes place from several metres to a few hundred metres from the nest, much greater distances than those between nests. Therefore females are as likely to interact with individuals from any nest as with females in a neighbouring nest.

The levels of relatedness found are high enough to promote cooperative social behaviour through kin selection. Ideally, the reproductive costs and benefits incurred by females sharing nests should be measured; this was not done here. However, generalisations based on Hamilton's rule can still be made. The highest levels of relatedness would dramatically increase the range of cost/benefit ratios that would promote cooperation. Even the lower estimates would increase the range of conditions resulting in increased sociality compared to those imposed if unrelated females shared nests. The level of inbreeding noted in one aggregation could also promote social evolution under certain conditions (Michod 1982; Uyenoyama 1984). High levels of relatedness have also been found in a primitively social bee (Schwarz 1986, 1987), and are presumed, based on behavioural observations, to occur in a variety of nest sharing Hymenoptera (see Michener 1974; Evans and Hook 1986).

Nest sharing appears to be at least correlated with relatedness. Preferential associations of relatives away from natal nests in some primitively eusocial *Polistes* spp. (West Eberhard 1969; Strassmann 1979), and the primitively social *Exoneura bicolor* (Schwarz 1986, 1987) and one aggregation of *C. antipodes* suggest an important role for kin selection in promoting nest sharing. Two lines of evidence could refute relatedness as an important factor in the evolution of nest sharing. One is a species where nonrelatives consistently share nests. The other is a demonstration that the benefits of nest sharing are of more importance than the relatedness component in Hamilton's rule.

Acknowledgements. The New South Wales National Parks and Wildlife Service allowed collection of the wasps through permit B263. Simon Easteal gave generously of his time and facilities as I learned the techniques of electrophoresis. Stuart Kohlhagen and Ian Boussy provided continuing advice. The laboratories of C. Bryant, A. Cockburn, M. Howell, P. Janssens and J. Oakeshott made available equipment and chemicals. Ross Crozier and Mike Schwarz provided the computer programmes. Andrew Cockburn, Penny Gullan, Ian Naumann, Mike Schwarz and Chris Thomson made useful comments on the manuscript.

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